

# The Use of the Foot and the Captacula in the Feeding of *Dentalium*

(Mollusca : Scaphopoda)

BY

LOUIS F. GAINEY, Jr.

Department of Biological Science, Florida State University, Tallahassee, Florida 32306

(5 Text figures)

## INTRODUCTION

SCAPHOPODS, COMMONLY KNOWN as Tusk Shells, are, as a class, the only exclusively infaunal marine mollusks; they are worldwide in distribution and have an elongate conical shell that is open at both ends. There have been three different feeding mechanisms described for the genus *Dentalium*. YONGE (1937) stated that detritus brought through the smaller shell opening into the mantle cavity with the respiratory current provides a source of food in addition to that obtained by the captacula. MORTON (1959) postulated that the captacula collect Foraminifera on their pad-like tips by a combination of suction and mucus. The captacula then retract into the mantle cavity where the food is transferred to the proboscis. DINAMANI (1963) described another mode of feeding in which small particles of detritus are carried up the length of the captacula by cilia. In none of these descriptions were the organisms observed feeding in their natural position, that is, buried in the substratum. Therefore, the purpose of this study was to observe the feeding of *Dentalium* while the animal was more normally oriented and to resolve the discrepancies reported by previous investigators.

## MATERIALS AND METHODS

Living specimens of *Dentalium* (*Antalis*) *pseudohexagonum* Ihering (HENDERSON, 1920: 46) and *D. (Graptacme) eboreum* Conrad, 1846 (HENDERSON, *op. cit.*: 66) were dredged in the channel of the Edward Ball Marine Laboratory at Turkey Point, Franklin County, Florida. Specimens were kept in small glass containers with flat sides and filled with sand from the channel. The chambers were placed in a 2-gallon capacity aerated aquarium. Observations were made with a Wild dissecting microscope mount-

ed horizontally. Observations of feeding behavior were made with the animal buried in the sand next to the wall of the container, although manipulation of food within the mantle cavity was observed in a living specimen which had been removed from its shell.

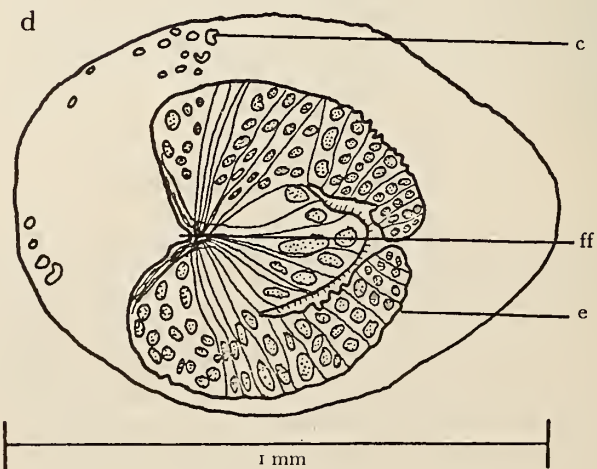
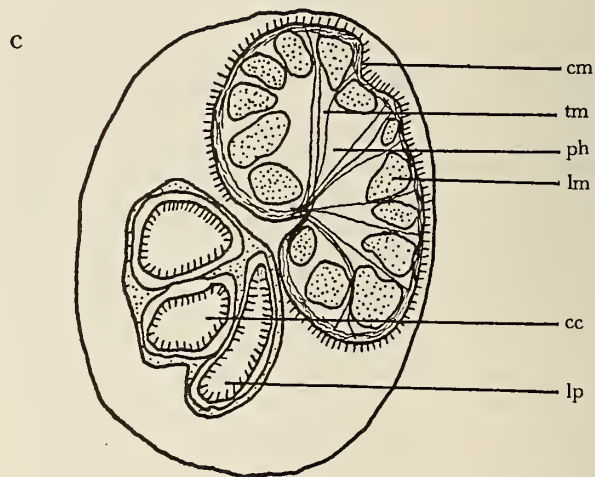
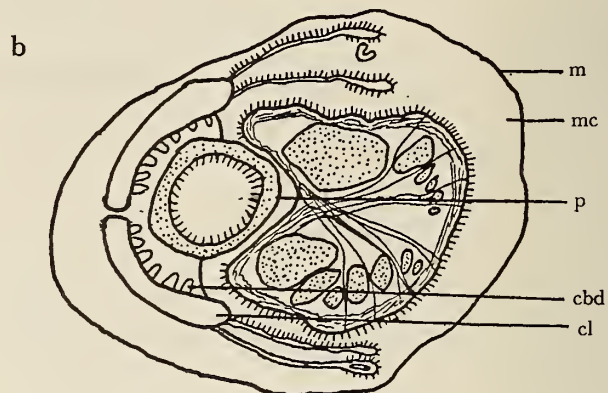
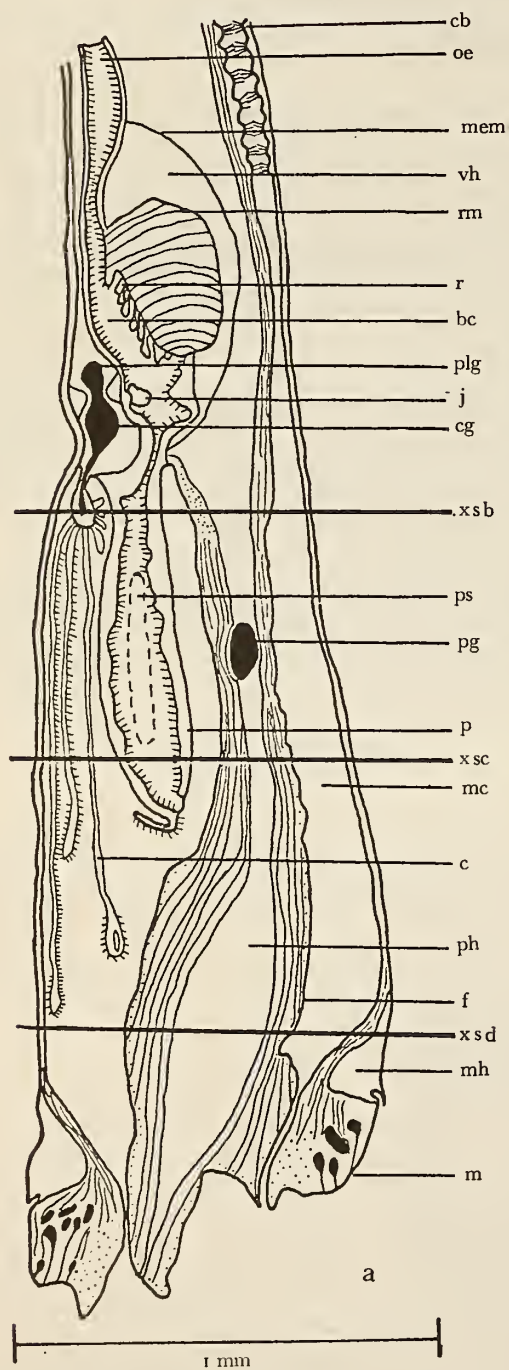
Several specimens of *Dentalium eboreum* were sectioned, and stained in Mallory's triple stain to observe general anatomy and histology. A few sections were stained with Periodic Acid Schiffs (PAS) and Alcian Blue as a test for mucus.

## OBSERVATIONS

**Anatomy:** The foot of *Dentalium eboreum* resembles that of other members of the genus (Figure 1). There are 2 epipodial lobes (e) near the tip of the foot which assist the animal in burrowing; dorsally there is a furrow (ff) which runs from the region of the epipodia to the base of the proboscis. This furrow and the epipodia lack cilia; the rest of the foot is covered with cilia that sweep particles into the foot furrow.

The proboscis (p) extends forward from the posterior end of the mantle cavity and is dorsal to the foot. The mouth (m), located at the tip of the proboscis, is surrounded by 5 lips (l) which resemble the leaves of a tree (Figure 2). The cilia on the margins of the lips pass particles towards the groove, where cilia beat towards the mouth. Lateral to the central cavity of the proboscis (cc) is a pair of pouches (Figure 1, c). These pouches (lp) are lined by a ciliated epithelium which, according to LACAZE-DUTHIERS (1856), is secretory.

The captacula (c) arise from 2 bands of tissue (cl), in the shape of a horseshoe, above the proboscis (Figure 1, b). The tip of each captaculum is expanded and bears a trough, termed the alveolus (Figure 3, a). The entire tip



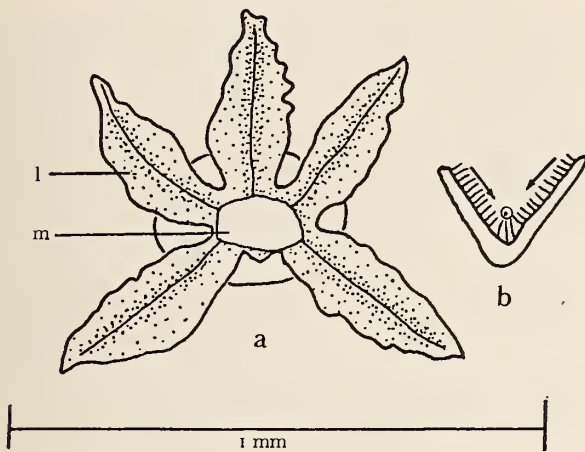


Figure 2

a: anterior view of the proboscis showing relationship of mouth (m) to the lips (l)      b: cross section of a lip showing direction of ciliary tracts

(t) and the alveolus (a) are covered with long cilia. The filament (fil) also bears cilia which form a tract (ct) leading from the base of the alveolus. Each captaculum has a ganglion (g) in its tip which is connected to the body of the animal by a nerve passing through the center of the filament. The tip also contains a number of large mucous cells (sc) that surround the ganglion; these cells bear ducts (sd) opening into the alveolus. Staining with PAS indicated that the secretory cells produce a mucin of neutral pH containing a large number of vicinyl hydroxyl groups. Several longitudinal muscle fibers (lm) pass through the filament to the base of the tip where

(← on facing page)

Figure 1

a: sagittal section of *Dentalium eboreum*; b, c, d: cross sections at levels indicated on "a"

bc - buccal cavity      c - captaculum      cb - ciliated bands  
 cbd - captaculum bud      cc - central cavity of proboscis  
 cg - cerebral ganglion      cl - band of tissue giving rise to captacula  
 cm - circular muscle      e - epipodium      f - foot  
 ff - foot furrow      j - jaw      lm - longitudinal muscle  
 lp - lateral pouch of proboscis      m - mantle      mc - mantle cavity  
 mem - membrane separating pedal and visceral hemocoels  
 mh - mantle hemocoel      p - proboscis      pg - pedal ganglion  
 ps - slit between lateral pouch and central cavity  
 ph - pedal hemocoel      plg - pleural ganglion      r - radula  
 rm - radula musculature      tm - transverse muscles  
 vh - visceral hemocoel

they branch into small bundles. The entire captaculum is permeated by connective tissue which may function to re-extend the longitudinal muscles (MORTON, 1959).

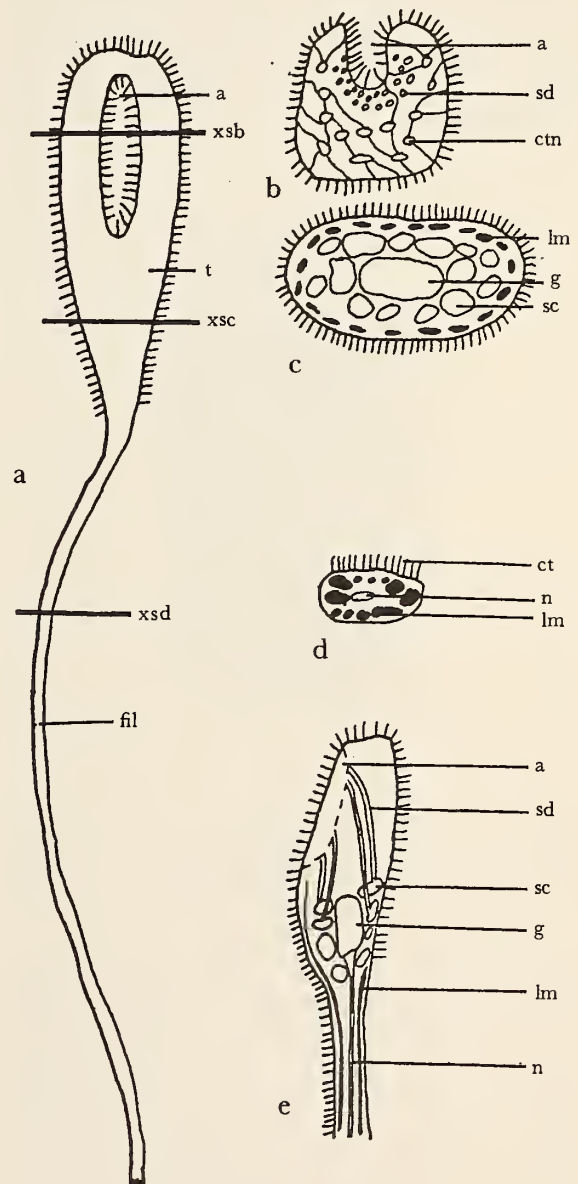


Figure 3

a: distal portion of a captaculum      b, c, d: cross sections of a captaculum at levels indicated on "a"

a - alveolus      ct - ciliated tract      ctn - connective tissue nucleus  
 fil - filament      g - ganglion      lm - longitudinal muscle  
 n - nerve      sc - secretory cell      sd - secretory duct      t - tip



**Feeding:** When buried in sand, both *Dentalium eboreum* and *D. pseudohehexagonum* lie with the dorsal surface up. The apex of *D. eboreum* lies beneath the surface of the sand, an observation which has not been reported before, while that of *D. pseudohehexagonum* lies above the surface. However, the distance which *D. eboreum* lies below the surface and *D. pseudohehexagonum* above the surface is variable. A small cavity in the sand, about the size of the expanded foot, was present at the anterior end of both species (Figure 4).

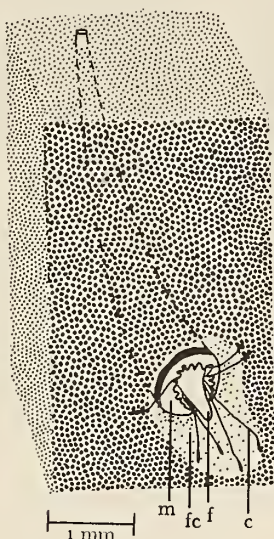


Figure 4

Diagrammatic representation of *Dentalium pseudohehexagonum* in the substratum

c - captaculum      f - foot      fc - feeding cavity      m - mantle

The foot has several functions with respect to feeding. Its primary one is burrowing downwards, which enables the animal to penetrate the substrate and obtain food (TRUEMAN, 1967). Movement in an upward direction was also observed and has not been previously described (Figure 5). The cycle begins with the slow extension of the foot out of the mantle cavity. The second step consists of the expansion of the tip and epipodial lobes of the foot. The third step occurs as the circular muscles of the foot contract, resulting in pedal extension, the animal moving backwards (up) in the sand. This is possible since the tip of the foot and the epipodia are expanded to form a firm anchor in the substratum. The last step occurs as the tip of the foot and the epipodia are collapsed. This shifts the anchorage from the foot to the shell. This cycle was

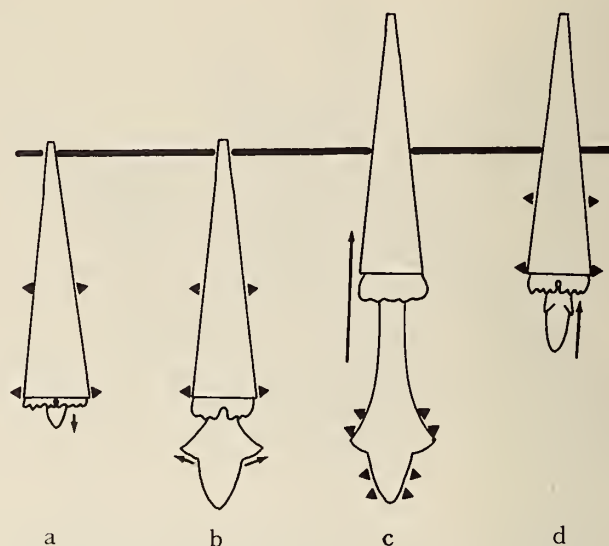


Figure 5

Diagram illustrating the steps in reverse burrowing  
a: slow extension of the foot out of the mantle cavity    b: pedal expansion to form a penetration anchor    c: movement of shell in a posterior direction    d: pedal retraction with the shell acting as terminal anchor. Black triangles indicate points of anchorage in substratum. Arrows indicate direction of movement.

usually repeated several times; the animal would then burrow back down into the substratum, but at a different angle than before. This whole sequence moved the animal to a new feeding area.

A second function of the foot is the preparation of a feeding cavity. After the animal has burrowed, the foot makes probing movements similar to those that take place during burrowing. The probes which construct the feeding cavity, however, are perpendicular to the major axis of the body and are made in a circle around the body. These probes pack the sand; the end result is a cavity similar to that pictured in Figure 4. The rhythmical probes of the foot pass detritus back along its surface. Most of these particles fall off; however, some of them are passed to the foot furrow where they are ingested by the proboscis.

When the animal is in a feeding position, the foot makes slow rhythmical movements in and out of the mantle cavity. These movements consist of a slow extension and dilation of the foot followed by a faster withdrawal. The movements are generally slow and serve to expel water in a posterior direction through the smaller opening of the shell. Occasionally, these movements are more intense and particles of sand and detritus are sucked

into the mantle cavity from the feeding cavity, where they are gathered by the captacula and the cilia on the foot. This process is similar to that observed by DINAMANI (1963), although his observations were not made on a buried animal. The dorsal foot furrow functions as a collecting site for food; particles brought into the mantle cavity by the captacula were observed to fall frequently onto the foot where they were swept up by the lips of the proboscis and passed to the mouth.

The captacula have two basic modes of gathering food. When *Dentalium* was observed feeding, numerous captacula were extended from the space between the mantle and the foot. Most of these captacula probed the walls of the feeding cavity with their tips, while the filaments were stretched taut between the tips and the mantle cavity. The tips moved over the walls of the cavity with the alveoli pressed against the substratum. The alveoli opened and closed, which resulted in small particles of detritus being swept into the alveoli by cilia and passed back along the filament to the mantle cavity. Observations on a dissected living specimen suggest that once inside the mantle cavity the particles fell onto the foot or were wiped off by the lips of the proboscis or other captacula. In the latter case, the shorter captacula, which remain in the mantle cavity, pick particles off the extended captacula. Masses of detritus were observed being passed towards the mouth from one captaculum to another. These masses may have been formed by the accumulation of small particles by the shorter captacula. Periodically, one of the extended captacula was observed withdrawing with its tip wrapped around a large particle. This mechanism was proposed by MORTON (1959), although he never observed its occurrence.

During burrowing, the cycle was periodically interrupted, and several captacula extended into the substratum; the animal would then prepare a feeding cavity, or burrow to a greater depth where the process was repeated. Intermittently during feeding, several captacula extended in groups into the sand above the feeding cavity. These captacula withdrew rapidly, dislodging detritus and sand from the roof of the feeding cavity. This sequence placed the particulate material in the bottom of the feeding cavity where other captacula could probe it for food.

## DISCUSSION

*Dentalium eboreum* lies buried with the apex of the shell beneath the substratum, while *D. pseudohehexagonum* is buried with the apex exposed. The situation in *D. eboreum* may conceal the animal from epibenthic predators. *Dentalium eboreum* might filter-feed from the respiratory

current as proposed by YONGE (1937) for *D. entalis*; if *D. eboreum* does feed by this method, then the position of the apex beneath the substratum could be an adaptation to bring particulate matter from the surrounding sand into the respiratory current. No evidence was found, however, to suggest that either *D. pseudohehexagonum* or *D. eboreum* feeds by means of the respiratory current.

Previous descriptions of burrowing accounted only for the downward movement of the animal into the substratum. With the discovery of reverse burrowing the life style of *Dentalium* comes into sharper focus. Not only can the animal burrow down into the substratum, but it can periodically move in reverse to a shallower depth, then burrow back into the substratum at a different angle or direction than before. The dynamics of moving in reverse are scarcely different from those described for forward burrowing by TRUEMAN (1967). The foot, in forward burrowing, forms a terminal anchor which acts as a fixed point when the shell and body are retracted into the substratum; the shell forms a penetration anchor which acts as a fixed point during extension of the foot. In reverse burrowing, the foot forms a penetration anchor, while the shell forms a terminal anchor.

DINAMANI (1964) suggested that the feeding cavity serves primarily as a space for food to filter in from the surface. I propose that its major function is to provide an exposed surface for the captacula to browse upon. In order for the ciliary mechanism of captacular feeding to be functional, the captacula have to remain straight. When extended into the sand the captacula are curved and twisted and are non-functional as ciliary feeding organs. Acquisition of larger particles by the tips of the captacula was not observed among those captacula which were extended into the sand. Presumably there is too much resistance encountered from sand grains for a captaculum to retract with a large particle on its tip. The predominance of feeding by means of ciliary tracts over the capture of large particles by the alveoli is most likely a function of the concentrations of the various types of food, smaller particles being dominant in the sand used in the observation tanks.

In addition to their role as feeding organs the captacula also have a sensory function. This was deduced from the presence of a ganglion in the tip of each captaculum and the captacular probing movements described in conjunction with burrowing. These probes could test the suitability of the substrate for feeding. If food is present, the animal will stop burrowing and prepare a feeding cavity; if food is lacking, the animal will burrow to a greater depth.

The presence of two different feeding organs, the foot and the captacula, raises the question as to which is the primitive feeding organ. The major function of the foot



is burrowing. The role of the foot in feeding may have evolved concurrently with the evolution of the feeding cavity. Although the captacula originally may have been sensory tentacles, they are probably the primitive feeding organs in the Scaphopoda. The capture of large particles by the captacula is perhaps the more primitive captacular feeding mechanism as suggested by the presence of the well developed radula for handling such particles. Ciliary feeding on small particles may have evolved as an adaptation to living in sand containing a high percentage of

detritus. In conclusion, observations of *Dentalium eboreum* and *D. pseudohexagonum* clearly show that they feed by a combination of captacular mechanisms rather than a single one as implied by the works of MORTON (1959) and DINAMANI (1963).

### ACKNOWLEDGMENT

I would like to thank Dr. Charles R. Stasek for his help and suggestions in preparing the manuscript and figures.

### Literature Cited

- DINAMANI, P.  
 1963. Feeding in *Dentalium conspicuum*. Proc. Malacol. Soc. London 36: 1-5  
 1964. Burrowing behavior of *Dentalium*. Biol. Bull. 126: 28-32  
 HENDERSON, JOHN B.  
 1920. A monograph of the East American scaphopod mollusks. U. S. Nat. Mus. Bull. 111: 1-177  
 LACAZE-DUTHIERS, FELIX JOSEPH HENRI DE  
 1856. Histoire de l'organisation et du developpement du Dentale. Ann. Sci. Nat. Zool. 6 (4): 225-281  
 MORTON, JOHN EDWARD  
 1959. The habits and feeding organs of *Dentalium entalis*. Journ. Mar. Biol. Assoc. U. K. 38: 225-238  
 TRUEMAN, E. R.  
 1967. The burrowing process of *Dentalium* (Scaphopoda). Journ. Zool. 154: 19-27  
 YONGE, CHARLES MAURICE  
 1937. Circulation of water in the mantle cavity of *Dentalium entalis*. Proc. Malacol. Soc. London 22: 333-336

